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THE CARE AND MANAGEMENT OF CAPTIVE CHIMPANZEES WITH SPECIAL EMPHASIS ON THE ECOLOGICAL ASPECTS

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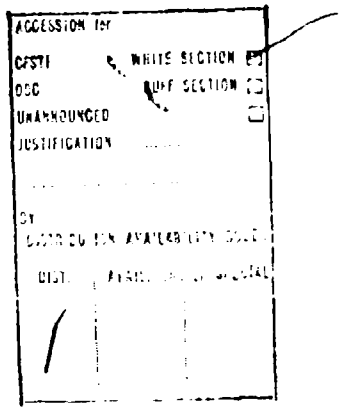

FOREWORD

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ABSTRACT

There are indications that present methods for the care and management of captive chimpanzees are not fully adequate, particularly from an ecological point of view, resulting in a physiological and especially psychological condition of the animals which is below optimal. In contrast to what is reported from the wild, many captive animals become apathic and dull, indulge in stereotypic behavior patterns and become very aggressive and impredictable as they get older. The fact that the present reproduction rate in captivity appears much too low to make a continuous importation from the wild unnecessary was also regarded as significant in connection with the conditions of captive chimpanzees. These points and their causes as well as possibilities for improvement are discussed in this report.

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I

INTRODUCTION

There appears to be a more or less general feeling that the present way of keeping chimpanzees in captivity is not fully adequate. Kortlandt (1, 2) has listed a number of phenomena that would indicate this.

(1) With increasing age chimpanzees tend to become dull and morose creatures, indulging for a great part of their time in stereotypic behavior patterns like rocking, masturbation, coprophagy, etc. These have not been reported in studies of chimpanzees in the wild (3, 4, 5, 6). Under natural conditions they appear to be lively, inquisitive and boisterous creatures.

(2) In captivity adult chimpanzees tend to become very aggressive and to have impredictable fits of temper. Many zoo people believe that it is impossible to keep more than one adult male chimpanzee in one and the same enclosure. In the wild, on the other hand, overt aggression appears to occur relatively rarely.

(3) Far more chimpanzees are imported to stock zoological gardens and laboratories than are born in captivity. According to Kortlandt (2) it even seems impossible to breed sufficient animals in captivity to maintain the existing stock, suggesting that the mortality is much higher than the natality, in spite of veterinary care and safety from the hazards of wild life.

Kortlandt (2) lists a number of reasons which would explain the present situation.

(1) The existing housing conditions at most zoos, and especially at primate research laboratories, are such that chimpanzees can only be kept solitary, in pairs, or in very small groups, so that their social needs are not met and chances for reproduction are low.

(2) These conditions also afford a minimal opportunity for intellectual employment and distraction (7). Furthermore, since chimpanzees are specialized long-distance walkers their locomotory needs would not be satisfied.

(3) Although chimpanzees appear to be very eurytopic animals they appear to be rather sensitive to heat (3). In the selection of laboratory sites and the design of cages this fact would be reckoned with insufficiently.

(4) Chimpanzees are omnivorous animals which, in the wild, select a great variety of food items. A too great food monotony in captivity could result in a sub-optimal condition.

(5) Especially in the United States animal keeping has a low status, resulting in relatively low salaries and consequently in a keepers' staff of relatively low education.

In this report the points put forward above will be investigated and methods for improvement will be discussed. Comment will be made particularly from an ecological point of view.

Possibilities for improvement in connection with factors more or less directly affecting the physical health of the animals, received ample attention in the literature. As the knowledge about the natural ecology of the chimpanzee, apart from the pioneer study by Nissen (3), is still of a comparatively recent date, it is not surprising that psychological and ecological factors were given less consideration. A second reason may be that in traditional animal husbandry psychological and ecological considerations were of little importance for those animals were selected originally for domestication which fitted in easily with the surroundings offered by man. Selective breeding has adapted them more and more to increasingly artificial surroundings and has reduced their ecological specificity (8,9).

Improvement in the ecological conditions of captivity can ensure that the animals remain "normal" (or healthy) in both physical and psychological respect. It is possible that there are areas in physiological and medical research where psychological health is more or less irrelevant, but it is a condition for at least some psychological and ethological research. And as it is practically impossible to conduct all, especially experimental, psychological and ethological research in the wild such improvements seem to be well justified for both zoos and laboratories.

The improvements would be even more justified if they had a beneficial effect on the reproduction rate. The increasing value of the chimpanzee in medical research may grow to be a threat for its

survival (10). According to Kortlandt (2) the present exportation rates have a devastating effect on the chimpanzee populations in many of the areas where they occur. The scientific responsibility requires that the main users of chimpanzees, laboratories and zoos, look for means by which exhaustion of resources can be prevented. Apart from designing and, more important, actually making use of capturing and transporting techniques that are less devastating than the present ones, also the establishment of large captive breeding colonies could be effective.

Fortunately, there is a growing appreciation of the problems mentioned. This is illustrated, for instance, by the plans that are being developed at Holloman Air Force Base, which, so far, have materialized in the "Consortium" (see II.B.2);

II

EXISTING HOUSING CONDITIONS

A. Zoological Gardens

The housing conditions in zoos and laboratories in general show some differences. In zoos there is always a concern about the public irrational appreciation of the housing conditions of the different species. Apart from efforts to make the animal surroundings resemble as closely as possible the supposed appearance of the natural habitat - to the extent even of creating small replicas of the normal biocoenos - attempts are made to build enclosures and cages that are pleasant by purely anthropomorphic standards. Thus, for instance, separating devices are made which least accentuate the state of confinement; enclosures are designed which are or look spacious and the layout of the landscape is such that it offers variation in appearance.

The results may be agreeable quasi-natural surroundings. And even if their design was but partly influenced by considerations of an ecological nature, such surroundings suitable by anthropomorphic standards, might in some cases by consistent with the ecological needs of the species. Particularly the anthropomorphic and the chimpomorphic idea of agreeable surroundings might well run parallel to a considerable extent.

Yet it is the great apes that have least of all zoo animals profited by this development. Although great progress has been made in the field of diet, hygiene, prophylaxis and therapy in connection with diseases, the environmental living conditions in most zoos are much the same as 50 years ago. It is only recently that new ideas are realized and that the building of "Freianlagen" has caught on. See the International Zoo Yearbook, 1959 (11). Yet, as far as I know, there is presently only one zoo that has a setup in which a group of chimpanzees is housed together. Most zoos have a number of inside and outside cages which are comparatively large if the greatest diameter of such a cage exceeds 30 feet. There is considerable variation both in layout and technical details as well as in the availability of climbing and manipulating devices. Yet most zoo cages are fundamentally similar to the units in the primate centers. However, the zoo cages are usually much larger.

B. Laboratories

Here the nature of the housing conditions are, naturally, to a large extent determined by considerations of efficiency. The amount of labor involved in caring for a, usually, large number of animals and in maintaining the cages should be kept as low as possible. It is, moreover, very important that the animals can easily be used for experiments and with as little stress as feasible. There must be opportunity to catch them without causing much disturbance. For a number of research projects it is necessary that high standards of hygiene are maintained and that several aspects of the animals physiology can be kept under full control. These factors favor the selection of rather small cages, as "clean" as possible in every respect.

It is therefore not surprising that in the few institutes I visited, and where research on chimpanzees was done on a large scale, the majority of these animals were housed singly or in groups of two, or sometimes three individuals in cages which apart from differences in detail were more or less equal in size and construction.

1. Conventional Cages

The dimensions of the inner cages were found to vary from 10 by 10 by 10 feet in one of the laboratories to 5 by 5 by 6 feet in another. The cages were surrounded by massive, painted or tiled walls, except on the side of the service corridor where the separation was of a heavy metal construction. In most cases it allowed an unobstructed view into the corridor. Only in one laboratory were the roofs made of metal meshes enabling the chimpanzees to climb and to hang from them. The equipment of the cages was restricted to a concrete sleeping shelf (apart from the feeding and drinking mechanism).

The outer cages were of a basically similar type. The dimensions varied up to 15 by 10 by 10 feet. Roofs and separations between cages were generally made of wire mesh. Solid constructions were less common. Here visual contact between neighbors was possible. Floors were of concrete, an easy and hygienic material, but for the chimpanzees hardly exciting. Only in a few cases could some neighboring cages be connected by means of slides to form larger units, and to allow the formation of groups of animals larger than two or three individuals. The majority of cages were facing south and fully exposed to the sun. Sometimes a rubber tire was attached to the roof so as to give the animals an opportunity for exercise.

2. Large Compounds

The large majority of animals were housed in the conventional type of cage. In addition each laboratory possessed or was constructing a larger enclosure for keeping greater numbers of animals.

Two compounds were basically similar, differing only in size (one measuring 400 by 100 feet, the other 100 by 100 yards). The areas were surrounded by a metal fence, the lower part of wire mesh, the upper part of solid metal sheets. Heights were about 5 m and 4.50 m. The lower fence was crossed twice by a chimpanzee; on one occasion it was observed that it got out at the corner. This compound will therefore only be used for temporary behavioral studies on small groups of young chimpanzees. Originally both compounds had trees present providing ample shade. In one, however, they had all died, owing to the damage caused by the inhabiting primates. There were no additional sun shelters in the outer enclosure; the vertical metal sheets of the fence gave only little shade during the hours that it was needed most. A small building at the side of both compounds contained an observation room, inner cages and service facilities. Both setups would allow permanent housing of six to nine chimpanzees. In the present treeless enclosure the inner cages did not meet the need for a cool sun shelter, since, being placed on the south side of a one-story building without air conditioning, these became quite hot.

The most ambitious project to date has been realized at the 6571st Aeromedical Research Laboratory, Holloman Air Force Base, New Mexico, with the construction of a Consortium which can house up to 30 chimpanzees. The outer enclosure is a circular area with a diameter of 1200 feet, surrounded by a concrete moat about 20 feet wide with sloping sides. About 40 feet outside this moat there is a 10-foot high fence with an electric wire on top.

Vegetation consists of low desert shrubs. These resisted the destructive activities of the chimpanzees in contrast with a number of trees planted in a system of ditches. Ten small open huts enable the animals to withdraw from direct sun radiation. Also, there is a small shady corner formed by the building containing the inner cages, which protrudes a bit into the outer area. Apart from some treatment and service rooms, this building contains two spacious dormitories

of about 45 by 14 feet. In each a wooden resting shelf 3 feet wide runs along one of the wall's full length through the room, mounted a few feet above the floor. The walls are of painted concrete. In these are a number of one-way windows for visual inspection.

Each room is connected with the outer area by a corridor. Both corridors lead through a restraint hall, where the corridors contain turnstiles. These can be fixed in given positions. A chimpanzee locked in a compartment thus formed, can be driven from here into a restraint cage. The corridors have stone walls, but the accessible roof is made of metal mesh. Thus a complete view of the corridor and turnstile compartments from above is afforded. Moreover, a water spray can be applied from above to influence the animal's movements. This construction, used to isolate animals from the group, appears to satisfy quite well in principle (see VI. B.1.).

A combination of the conventional cage types with compounds is being built at a laboratory that is planning to keep chimpanzees in the future. In the comparatively small setup each of a row of nine inner cages (surface: about 8 by 8 feet) will correspond to an outer cage of the same width, but greater depth. In front of these cages there will be a corridor completely enclosed by wire mesh, through which each of the cages can be connected to each of three large enclosures. The three enclosures, lying side by side, will be 215 by 50 feet. They will be separated by wire fence, 10 feet high, on top of which will be a 6-foot wide solid metal rim, sloping inward and forming an angle of 45 degrees with the vertical. At the top this metal strip will bend downwards. This edge, projecting down will be 5 inches wide. It is expected that this will efficaciously prevent animals that have climbed the fence from jumping to the rim to get a hold of it.

III

SOCIAL ORGANIZATION

The data resulting from the recent field studies (3, 4, 5, 6) show considerable agreement with respect to the social organization of the species. Data presented in this short survey, will be discussed in the following sections.

A. The Stability of Social Aggregations

In contrast to the previously accepted idea that chimpanzees live in "harem" or "family" groups, they appear to form highly unstable aggregations without a pronounced dominance hierarchy. Animals and groups of animals both appear to be able to join or segregate freely at any time. The impression exists that these groups are not part of a larger well-defined tribe, but that there is a continuous system of overlapping ranges, so that animals become progressively less familiar with each other the farther the centers of their ranges lie apart.

B. The Nature of Social Aggregations

Kortlandt (4) and Goodall (5) have distinguished two types of aggregations, namely nursery groups consisting of mothers with youngsters and adolescents, and sexual groups consisting of childless females and males. Both groups were quite different behaviorally. Reynolds and Reynolds (6) have distinguished four types of bands, merely on the basis of their composition:

(1) Adult bands, containing adults of both sexes and occasionally adolescents, but no mothers with dependent youngsters;

(2) male bands, containing only adult males;

(3) mother bands, containing only mothers with youngsters and, occasionally, other females;

(4) mixed bands, containing mothers with youngsters, childless females, adolescents and adult males.

They have counted the frequencies of those bands (see Table I) distinguishing between large bands containing seven or more, and small

bands containing six or fewer individuals (clinging youngsters have not been counted, and solitary males have not been taken as groups).

TABLE I. Frequencies of Occurrence of Different Types of Bands as Counted by Reynolds and Reynolds (6).

Large Bands (n >7):	Adults	26
	Males	1
	Mothers	4
	Mixed	51
Small Bands (n <7):	Adults	39
	Males	33
	Mothers	32
	Mixed	29

The figures show that adult groups and particularly mixed groups are comparatively large, whereas male and mother groups are small.

C. Population Composition

Each of the investigators has given sex-age ratios for the "resident" population at the observation area as shown in Table II. Since the authors use different age classifications the figures are not completely comparable. Kortland reckons immatures to be under 8-1/2 years of age and has counted adolescents (over 8-1/2 years old on the average) as adults. In the classification of Reynolds and Reynolds dependent youngsters are up to 6 years old; adolescence ranges from 6 to 8 years. In the classification of Goodall juveniles include animals up to 7 to 8 years. Adolescents range from 7 to 9 to 10 to 11 years. Both Reynolds and Reynolds and Goodall state that adolescence is the period during which the females develop sexual swellings. So there may be a slight difference in the age estimates each of them applies. We will therefore be near the truth if we simply add up the figures of the different classes referring to youngsters and adolescents and regard this as the figure representative for the class comprising the animals ranging from 0 up to 9 (Table III).

TABLE II. Sex-Age Ratios Given by Investigators

	Kortlandt	Goodall	Reynolds and Reynolds
Adult Males	12	> ? 15	> ? 20
Adult Females	18-21	> ? 16	23-30
(with children)	11-14	9	17-20
(without children)	7	7	6-20
Immatures (K)	19-21	14-20	
Juveniles (G)		10-20	
Adolescents (G)			
Dependent Youngsters (R)			17-20
Approaching Adolescents (R)			10-12
Unknown Sex (K)	2		

TABLE III. Sex-Age Ratios, Summated from Table II

Adult Males	> ? 47
Adult Females	> ? 57-67; with children - 37-43
Immatures	70-93

IV

THE LEVEL OF AGGRESSIVENESS

A. Aggressiveness in the Wild

There is a good deal of tolerance, according to Goodall (5), more so with the males than with the females. This is most obvious during the period from the beginning of August until the end of November when large temporary associations were formed and most matings took place. Signs of jealousy were not observed. Often, several males mated with the same female. Once seven males mounted one female one after the other with pauses of less than two minutes between the first five matings. Goodall noted a very low incidence of aggressive interactions. What is very probably high-intensity threat occurred on four occasions, three of which were caused by the observer throwing a banana between two animals. Attack was rare and only on one occasion was a fight seen between adult males.

Reynolds and Reynolds (6) observed only 17 fights or displays of threat during 300 observation hours. None lasted for more than a few seconds. Kortlandt (12) also mentions the low incidence of aggression. Yet chimpanzees are boisterous extroverts. Accumulated social tension frequently finds an outlet in impressive but harmless intimidation displays which occur especially in the sexual groups. The animals may chase each other, but the pursued is always faster and there are plenty of escape possibilities.

B. Aggressiveness in Captivity

The above picture is somewhat different from what one would expect on the basis of experience with captive chimpanzees. The way in which these animals are housed in most zoos expresses the conviction of most directors that it is impossible to keep chimpanzees in groups in captivity, or at any rate to keep more than one male in the same cage. This is certainly true in connection with the usual type of relatively small cages. However, experience at the Chester zoo and the Consortium of the Holloman Air Force Base has taught that, if enough space is available, a large number of animals can live together comparatively peacefully.

C. Aggressiveness in the Holloman Consortium

During my stay at the Holloman Air Force Base for behavioral studies of the group in the large Consortium (see II.B.2. for a description) during the autumn of 1966, I got the impression, nevertheless, that there were still some differences as compared to the situation in the wild.

The colony contained 25 individuals. Table IV shows how these were divided over different age groups.

TABLE IV. Sex-Age Classification of the Colony in the Consortium of the Holloman Air Force Base During Autumn 1966

	Males	Females cycling	Females not cycling
Age: over 10:	2	3	
8:	2	2	
7:	1	1	3
6:	2	1	2
5:	1		2
under 5:	3		

If we place the line separating adults and immatures between 7 and 6 years of age (taking the two cycling females below the line for granted), the average age of the colony appears to be very young.

In comparison with the reports from the wild this colony appears to be much more aggressive. During approximately 200 hours of observation 84 recordings were made of aggressive interactions during which bodily contact occurred. Since it appeared not to be possible to score each aggressive interaction the number of such interactions occurring was definitely higher. In 61 of these one of the animals was hit and/or trampled. In five, both animals hit the other. In 16 interactions one of

the animals was bitten. In three of these cases an animal was torn at and bitten for many seconds, and blood was drawn. As a result of one of these cases an animal was so badly wounded on head, shoulders and especially the hands and feet, that it had to be removed from the colony for medical treatment.

D. Reasons for the Difference in Aggressiveness Between the Consortium Colony and the Studied Wild Populations

The great difference between these figures and those given by Reynolds and Reynolds (6) cannot be explained as a result of the difference in observation conditions, because all cases recorded involved intense vocalization, though sometimes lasting only a short time, and would therefore not be easily overlooked.

1. Food Competition

As the greater part of these interactions occurred during or around feeding time, it seems very likely that the social tensions due to the food-competition were discharged in this way. As food-competition hardly seems to exist in the wild, the difference with respect to the number of aggressive encounters could perhaps thus be understood. An argument in favor is that of the few instances of aggression recorded by Goodall (5) some were caused by food-competition. On one occasion an animal had a piece of meat and on others Goodall gave bananas when the aggression occurred.

2. Specific Sympathetic and Antipathetic Ties

It is questionable whether food-competition alone explains the phenomenon. Having been familiar with chimpanzee social behavior before I arrived at Holloman, I started to take behavior recordings long before I could recognize the animals individually. This was necessary since the period of my stay was relatively short. Consequently it is not possible now to establish accurately whether particular animals were extraordinarily aggressive and/or whether particular animals suffered a disproportionate number of attacks. Yet I may mention that I got the strong impression that certain individuals, for instance the adult male Albert (at times) and the almost adult female Elizabeth (almost constantly), turned out to be unprovoked (i.e. no direct visible reason) aggressors relatively frequently. Other animals, like the subadult

females Gigi and Rosemary, seemed to get an unfair share of the attacks. (Rosemary was the animal which had to be taken out after being injured by Albert.)

Besides antipathies there are certainly specific sympathies. Bobkowski (personal communication) has shown that particular animals are very often in association. An instance of such a mutual attraction is the obvious bond between the male Brownie and the female Grace and, when Rosemary was still present, between her and Brownie. Goodall (5) has also noted this phenomenon.

One may therefore assume that specific sympathies and antipathies exist both in the wild and in captivity. In the wild, however, the existence of antipathies would probably rarely find expression, since the animals involved can easily avoid each other, because of the overall loose social organization.

3. Disturbances in Social Adjustment Due to Previous Experiences

In the present case, however, something else may be involved as well. As will be discussed more extensively below under the section "Reproduction" most captive chimpanzees have been captured as babies and have grown up in a situation in which they may have been deprived from a multitude of social experiences which belong to their normal obtainments in the wild. To what degree this influences later social life, one cannot yet fully appreciate. It is striking, however, that of those animals, which have been mentioned above, Albert and Gigi were somewhat abnormal in other respects of their social life. Albert did not show a well integrated sexual behavior (see V.D.1.) and Gigi made a somewhat apathic impression. She seemed to be sitting alone rather frequently, meanwhile continuously rocking. Rosemary did not seem to be abnormal, but looked rather odd, because her head had been shaven in connection with experimentation. This raises the question whether abnormality in appearance evokes antagonism.

4. Unfamiliarity Still Due to Recent Formation of Group

Another possibility namely that the high level of aggression is only a transitory phenomenon still caused by the fact that the colony is not yet completely established (it was about 6 months old), can probably be ruled out, since it is in apparent contradiction with the fact that unfamilarity in itself under natural conditions does not seem to bring about aversion.

5. Lack of Space

It will be clear from the preceding points that the high level of aggressiveness of captive chimpanzees in a group is not only an effect of the lack of space as such. This is also suggested by the following. The surface of the outer area at Holloman is about 10 ha., (approximately 25 acres). The animals use only a part of it extensively, namely the quadrant which is nearest to the building. Only during the early and late hours of the day do the animals make a trip during which they explore the more distant parts. Occasionally, when animals are chasing one another, they may get rather far from the building as well.

In contrast probably to the situation in the wild, however, the different parts of the living area are greatly unequivalent, all vital facilities being concentrated at one point. This counteracts the tendency to form subgroups and to spread, and may thus be responsible for a somewhat higher tension.

E. Means to Suppress Aggressiveness

It is likely that the most fierce expressions of aggression can be suppressed by taking out particular individuals and/or exchanging them with other groups. Spreading of vital facilities, and changes in the feeding routine could lower the overall level of aggressiveness. Also, the layout of the landscape could be made to offer more opportunity for the animals to withdraw from one another's sight. These points will be treated more extensively in Section VI.

However, it is very unlikely that the aggressiveness could be lowered to the level found in nature by such measures. Antipathies would remain, and with the given conditions of captivity animals having a dislike for each other cannot avoid being in each other's neighborhood over and over again. This would not appear to be serious, however. The great majority of the aggressive encounters, spine-chilling as they may have been to a naive observer, did not have any serious effect, especially the hit and trampling interactions.

V

REPRODUCTION

One of the indications that there is still much wrong in the physical and/or psychological conditions of chimpanzees in captivity, is, according to Kortlandt (2), the fact that it still appears impossible to breed chimpanzees in such numbers that a continuous importation of animals from the wild to keep up the captive population becomes superfluous. His impression is that even in good zoos that want and try to breed, more chimpanzees must be bought than are born to maintain the stock. Unfortunately, there are no figures directly substantiating this point.

A. Natality in the Wild

No exact figures are known, but from Table III we can arrive at a minimum estimate for the percentage of births in the wild. The average total for the sample population is 190. An average of 81 members falls in the age class from 0 to 9 years. So the average number of births would be 9 per annum, i.e. 4.9 percent, if there were no infant mortality. It does exist, however. For instance, Goodall (5) mentions two females which were known to have lost very young infants (under 6 months).

In another way we may therefore arrive at a maximum estimate for the percentage of births. All observers saw a fair number of mothers with offspring. Based on the age differences between siblings, they arrived at a birth interval of about 3 to 4 years (average 3-1/2 years) if the preceding youngster survives; it will be shorter if the preceding youngster dies before the age of two. Let us assume, in order to make the estimate, that all females are fertile (which is most unlikely) and that a fertile female will breed regularly. We may say that in our sample population the 81 youngsters from 0 to 9 years of age have been born with an average interval of 3-1/2 years, thus requiring $3.5/9 \times 81 = 31.5$ females. So 31.5 females have 9 youngsters per year. If we assume that the youngsters of the remaining 30.5 females die shortly after birth, these 30.5 females could have 30.5 births per year. In total there would be 39.5 births per annum, i.e. 21 percent. A decrease in the number of deaths of very young infants is necessarily coupled with a decrease in natality. The real figure will, of course, be somewhere in between 4.9 and 21 percent.

B. Natality in Primate Laboratories

On discussing this subject one should distinguish between zoos and primate laboratories. First because most primate centers are relatively young and have only recently acquired their stock. The percentage of animals capable of reproduction is still comparatively low and on this basis alone one may expect a low birth record for these institutes for some time to come.

Secondly, it may be as is the case at the Holloman Air Force Base, that a certain number of animals are being used in experiments for which they have to be sacrificed or for which the survival chances are lower than normal. This may greatly affect the ratio of births versus imports.

So far only the Yerkes Laboratories which have existed for about 40 years can provide relevant data as to the number of births (Bourne, personal communication). Between 1930 and 1966 there have been 164 chimpanzee births, of which 23 were stillborn. With an average number of 55 animals in the colony this gives a yearly birth percentage of 8.3 percent. Comparison with the estimates for the wild shows that the birth rate at the Yerkes Laboratories has been of approximately the same order of magnitude.

C. Natality in Zoological Gardens

From data published in the International Zoo Yearbook, it is possible to give a reasonable estimate of the percentage of births in captivity. In the lists published in a number of subsequent editions the zoos have been given that have bred chimpanzees. In a few of these editions the numbers actually bred per zoo are given (see Table V).

For the years over which both numbers have been given the average number of zoos is equal to the average for all years and we may therefore assume that an average number of 21 chimpanzees bred per year is a reasonable estimate. Only for 1962 is the total number of chimpanzees in zoos known; it amounted to 504. We may take this as the average number of chimpanzees for the given years. It then follows that the average number of births is about 4 percent.

This figure is lower than the minimum estimate given for the wild (see Section V.A.).

TABLE V. Number of Chimpanzees Bred per Zoo

	Number of zoos having bred chimpanzees	Number of chimpanzees born
1959	13	?
1960	10	?
1961	20	?
1962	18	24
1963	16	19
1964	20	?
1965	17	20
mean	16.3	21

D. Reasons for Relatively Low Birth Rate in Zoos

There can be several reasons for the fact that the natality in zoos is still below the level in the wild.

1. Social Deprivation

It has already been suggested that the influence of previous experience can have a profound effect on later social adjustment, especially in the primates where the role of individual experience in shaping the behavior into a biologically adaptive and functional whole seems to be relatively great and may to a large extent be based on social traditions. Thus deprivation studies have shown that lack of contact with the mother during early infancy and, later, with age mates can have profound effects on socialization in adult life (for a recent review see reference 13). Most striking deficiencies manifest themselves in parental and sexual relationships. Mothers deprived of normal socialization experiences appear not to be able to raise their young. Deprivation effects on sexual behavior are most manifest in the males. Extreme playfulness or aggression may prevent any sexual intercourse. Often when the animals appear to be sexually stimulated, their sexual behavior patterns are very poorly integrated; frequently they revert to some stereotype form of masturbating behavior. This was seen, for instance, in the adult male Albert

of the Holloman colony. He would perform the sexual invitation patterns, but in reaction to a female's positive response start masturbation by sucking his own penis. I have seen similar things in a few zoo chimpanzees.

A young animal growing up in its natural surroundings continuously learns by its increasing participation in and witnessing of the interactions going on in its group. The tremendous interest on the part of youngsters and females for a mother and young and the excited interest youngsters have in sexual interactions (5) undoubtedly have significance.

The chimpanzees that live in zoos and laboratories usually lack these highly varied experiences. As a rule these animals have been collected from the wild when they were still babies. In a zoo or laboratory they seldom live in the company of adults. If not alone they grow up in the company of age mates. Moreover, from the moment of capture until the moment of placing it in its definitive captive surroundings, the baby chimpanzee has undergone an amount of stress which may well have long-lasting effects. (It would undoubtedly be so for a human in similar circumstances.)

The effect of social deprivation could be more serious in zoos than in laboratories because most zoos only possess a couple of chimpanzees. According to the 1962 census by the International Zoo Yearbook there were 504 animals, spread over 121 zoos, i.e. an average of 4.2 chimpanzees per zoo. If in such a case there is only one, unsuitable male, one or more females are automatically excluded from the reproduction process as well. However, in laboratories where many animals are present a recombination of animals may take place.

To prevent this gap in the experience of the growing animal, it might be recommendable to employ the method of procurement presently planned by the Southwest Foundation of Research and Education at San Antonio, Texas (Hummer, personal communication). It is planned to capture a number of animals of different age groups and sex at one and the same location. In this way one collects a group of animals sharing a more or less common social tradition; one gets the tradition along as well. That this is possible has been proved by Rollais (14). This method has been adopted by the station de Capture et d'Elévage at Epulu in the Congo (15). With the aid of Pygmies, nets

were placed around chimpanzee sleeping sites during the night. At daybreak, when the apes came down to the ground, they were chased into the nets by dogs. The animals which got entangled in the nets could then be captured. This technique, although admittedly more expensive, has another advantage over the conventional one in that it is much less devastating. For a full appraisal of this aspect the reader is referred to Kortlandt's (2) description of current techniques.

2. Lack of Social Stimulation

Both Goodall (5) and Kortlandt (16) have noted that sexual behavior in the wild has the character of some kind of "sexual riot", not unlike what is seen in dogs in the street. Signs of sexual jealousy are not obvious. From Table I it can be seen that chimpanzee bands in which adults of both sexes are present are clearly greater on the average than bands of other types. Goodall has noted that "from the beginning of August until the end of November the Gombe Stream chimpanzees move about in large groups much of the time. It is not known whether these groups are formed as a result of a need for contact stimulated by sexual excitement, or whether the increase in activity, due to the aggregation of a large number of chimpanzees has a direct effect upon sexual behavior . . . . . All copulations observed took place in this period and at the time when the animals concerned were part of a large group." Later she has witnessed a couple of copulations outside this period, which involved one female in estrus and two males.

These data lead to the impression that social factors characteristic for large bisexual gatherings may play an important part in the elicitation of sexual behavior. The fact that successful mating occurs, nevertheless, in zoos and laboratories in very small groups or pairs, shows that these factors are not or not always indispensable.

3. The Composition of the Zoo Population

The chimpanzee has been a very popular zoo animal for many decades. Nevertheless the total zoo population is growing continuously. In the first place the number of zoos is increasing constantly. In the 1962 edition of the International Zoo Yearbook, 356 zoos are listed. For 205 of these the year of foundation has been given. Of these 205 zoos, 138 were founded before 1945, 22 from 1946 until 1950, 20 from 1951 until 1955, and 25 from 1956 until 1960. Secondly, the number of zoos keeping chimpanzees may have increased considerably. There are no figures to show this, but from my own experience I know, that there

are several zoos founded before 1945 which have started showing chimpanzees in the period after World War II. For this reason the young age groups would be represented rather strongly and a relatively low birth rate could be expected. It would be of interest to investigate the demographic records of the zoos to see whether the difference in birth rate can be explained merely as an effect of the difference in number of females suitable for reproduction or whether it should also be explained in terms of some differential factors of an ecological or psychological nature.

E. Discussion on Reproduction

The total reproduction is a function of both natality and mortality. From the above computations it appears that the natality in the one elder primate research center has been quite satisfactory. In zoos it is lower than in the wild, although not tremendously. The difference with the wild may well be due to a different age composition of the zoo population and to the fact that the population is very much split up so that part of it may be excluded from reproduction by lack of a suitable partner. For the rest it may be due to psychological effects of the captive situation. It is difficult, however, to evaluate the importance of each of these factors at present.

In comparison with the number of births the number of imported animals is great. However, the exact figure of the latter is unknown. We can get an idea of the order of magnitude, nevertheless, from data collected by Boyle (personal communication) with respect to the traffic of chimpanzees through the Animal Hostel at London Airport, one of the main transito ports for these animals (see Table VI).

TABLE VI. Number of Chimpanzees that have Passed the London Airport Animal Hostel Between 1959 and 1966

1959	-	62
1960	-	31*
1961	-	44
1962	-	56
1963	-	48*
1964	-	109*
1965	-	253
1966	-	309

* approximate figure

The actual number of imports will clearly be higher, because not all animals stay at the London Hostel. The increase during the last three years is undoubtedly due to the strong growth in the use of chimpanzees for research. This is confirmed by data supplied by the United States Public Health Service (Eyestone; Hughes, personal communications). From July 1964 until December 1965, 168 chimpanzee imports were recorded; from July 1965 until June 1966, there were 286. Most of these went to the newly established primate research institutes. We may assume that the figures of the preceding years give a fair picture of the number of animals imported for zoos, and we may estimate the yearly average at about 50, i.e. about 400 animals during the last 8 years. When compared with the total number of chimpanzees in zoos which according to the 1962 census by the International Zoo Yearbook was 504 at that time, this seems to be a rather high number, even if we take into account that there has been an increase in the number of zoos keeping chimpanzees. An explanation would be that the mortality in captivity, especially of newly imported animals is comparatively high.

About the mortality very little is known, both from the wild as well as from captivity. From the estimated minimum and maximum birth rates presented above, we may arrive at a maximum estimate for the percentage of deaths in the age class from 0 to 9 years of age, namely about 75 percent.

For captivity there are some figures which suggest that in zoos the mortality is quite high. According to the 1962 census by the International Zoo Yearbook not more than 47 out of a total of 504 zoo chimpanzees were born in captivity. This seems to be rather low if we realize that from 1959 until 1962 at least 67 chimpanzees have been bred (see Table V). Moreover, breeding will certainly not have started as late as 1959.

This would suggest that to improve the reproduction rate and to alter the ratio between births and imports, mortality, particularly infant mortality should be given more serious thought than natality.

VI

THE DESIGN OF A HABITAT FOR CHIMPANZEES IN CAPTIVITY

Chimpanzees are kept in captivity with some purpose. It is therefore evident that the ideal chimpanzee habitat in captivity should guarantee that this purpose is reached most effectively and efficiently, and that the animals can develop in the most natural (i.e. normal) conditions possible.

For the zoological garden this is the least of a compromise. Its aim is to offer the opportunity for acquaintance with the different animal species. In contrast to the zoological museum it shows the live animal, i.e. with its behavioral characteristics. Thus it has at least to supply the realizable conditions necessary to maintain these characteristics.

However, in laboratories the compromise may be more difficult to realize for several reasons.

At present most animals are housed alone or in very small groups in rather small cages which contain a minimum of manipulation and exploration possibilities. Kortlandt (2) has stated that "since chimpanzees are specialized long-distance walkers, we cannot expect them to remain in good condition when kept in cages." One could object that they do not show by continuously pacing up and down, as is well known for many other animals (e.g. wolves and bears), that in this way some "locomotory drive" is being thwarted, at least not in the adult ones. Nevertheless the lack of locomotion may influence their physiology, as happens also in the other great apes which gain extraordinarily in weight in captivity.

More important, however, it seems that, without the company of more than one animal they lack the diversity of social contacts which they experience when living in a group. As there is also no possibility for any intellectual employment and they completely lack the challenges which are part of the daily routine in the wild, one should regard alerting social interactions even more important for them as a compensation. Thus Kummer and Kurt (17) have found on comparing the behavior of hamadryas baboons in a captive colony and in the wild that the repertoire of social behavior patterns was richer in captivity and that the amount of social interaction, notably of play, was greater. We have already elaborated on the consequences which a socially deprived environment might have for the reproduction of these animals.

A. Groups of a Natural Structure

In accordance with the situation in the wild one would prefer to see the chimpanzees, and not just a small part of the total population, housed in the kind of conditions offered by the Consortium at the Holloman Air Force Base. A group should not contain many more than 25 individuals, which is about the usual maximum of sexual groups (5), and it should have an age composition comparable to the one given in Table III. It would be ideal if at least part of the group still possessed the treasure of natural social experiences and traditions, because it was captured as such in the wild.

B. Objections Against a "Natural Group" Setup

1. Isolation of Animals

If we exclude financial objections against such a setup, there remain a few, especially in connection with the use of chimpanzees in laboratories. I have mentioned already that for a number of projects individual control of the animal is necessary which is only possible if the animal is kept isolated. Therefore, there must be facilities for this.

For the majority of projects a continuous isolation is not necessary. However, it must be possible to separate an animal from the group quickly and without causing stress when it is needed for an experiment. This seems to be a laborious task. On the occasions I have witnessed such an operation in the Holloman colony, however, I was surprised by the speed with which it could be carried out. The principle involved, namely a turnstile device between the inner and the outer cage in which an animal can be held and from which it can be driven into a transport cage (see Section II.B.2.), has certainly stood the test. The turnstile is used normally very frequently by the animals when going from the inside cage to the outside and vice versa. They are familiar with people walking on the top of the corridor system and do not hesitate to enter it even then. If the frequency of capturing procedures is not too high there should be no reason to fear that a rising aversion will prevent the animals from passing through when they notice that a capturing procedure is to be going on. If necessary they can be forced to go through by means of a water spray or a cloud of carbon-dioxide from a fire extinguisher. If an animal is to be used rather frequently then it could be separated temporarily during the period of experiments.

Since in the wild, temporary dissociations of groups are common, it is likely that reintroduction of an animal into the group, after some time of separation, does not cause trouble. The experience at the Chester Zoo is in agreement with this (Mottershead, personal communication). Of the few reintroductions that I witnessed at Holloman, only the one of the big "dominant" male Sampson caused general excitement. This agrees with Goodall's (5) observation that the joining of two groups evokes more excitement the more adult males are involved in the meeting.

2. The Tractability of Experimental Animals

The present experimental procedures involve considerable handling of the animals. It belongs to the normal routines that the animals are dealt with frequently in order to keep them docile and tractable and to ensure that a comrade-like relationship with the handlers is established. The experience at the Holloman Air Force Base is that this is much more difficult if the animals live in a group. The handlers are at once "outsiders."

This appears to be a serious objection. To overcome it one could either devise handling routines for which it is irrelevant whether the animals are tractable or not, or one could incorporate facilities in the setup of the compound which allow individual separation so that frequent handling sessions become possible.

3. Birth in the Group

So far no one has had experience with births within a group. At the Chester Zoo the females bore their young in isolation. Yet it is Mottershead's opinion that this is not necessary (personal communication). In the wild the pregnant females obviously withdraw from the mixed groups to join mother groups. Especially if relatively low-ranking females are concerned it may, therefore, be wise to have a possible plan to isolate the animals. It may be recommendable, however, to allow visual contact between the group and mother and young and to have an opportunity for gradual introduction, namely a room in which mother and young can meet selected group members.

4. Introduction of a New Animal in an Established Colony

Gradual introduction or successive introduction to each of the group members seems advisable for a newcomer into an established

group. On a few occasions that a newcomer was placed abruptly together with all the members of the Holloman colony, a tremendous mass intimidation occurred. This type of reaction against a newcomer seems contradictory with the data from the wild concerning the joining of individuals and groups. However, it is not likely that in the wild a complete stranger would venture to enter a mixed group.

C. A Combination of Consortium and Conventional Cages

Many of the objections against the Consortium can be overcome by incorporating the opportunity to isolate animals. An ideal setup would therefore consist of units, each containing a large open enclosure and one or more dormitory halls for normal use, and 10 to 12 smaller cages permitting the isolation of the group members. It could house a maximum number of 25 animals, i.e. some two animals per small cage.

It has the advantage that all the animals or some of them can be lured into the cages at feeding time for individual feeding. A speedy operation could perhaps be obtained by marking all cages in a different manner; by means of a conditioning technique each of the animals could be accustomed to enter a particular cage. In this way one can ensure that every animal gets its proper food ration. This is sometimes a problem at Holloman with the present setup, especially in connection with some members of the intermediate age classes.

D. Visual Barriers in the Enclosures

One of the problems connected with keeping a number of animals in a group in captivity is that animals that are adverse to each other cannot help being in contact with each other almost continuously. To avoid constant visual contacting and at the same time to enhance the variation in the landscape, earthen walls could be constructed in the outer cages and valleys in between. Care should be taken however, that an observer has a view of the entire area and can follow an individual animal wherever it goes so that, amongst other things, behavior study remains possible. The earthen walls could be situated in such a manner that these radiate outwards from the point of observation. If this is some yards above ground level, a circular wall could be made close to it to prevent an animal below the observation stand from seeing all the others at once (Fig. 1). Under Section IX, "Climatological Conditions" I shall discuss the desirability of a sun shelter in the form

of a large platform on columns. This again should not hinder observation. If the construction is such that the animals can climb on top of it, a heighth somewhat lower than the observation level should be chosen, so that both the area behind it as well as the upper side of the platform remains visible (Fig. 2). If there is only one dormitory per unit, the presence of visual barriers is even more necessary. They could be in the form of screens. Again their position should be considered carefully. Firstly because they should not hinder observation; secondly because they should not introduce even more dead corners (the screens should not be connected with the walls, enabling the animals to walk around them).

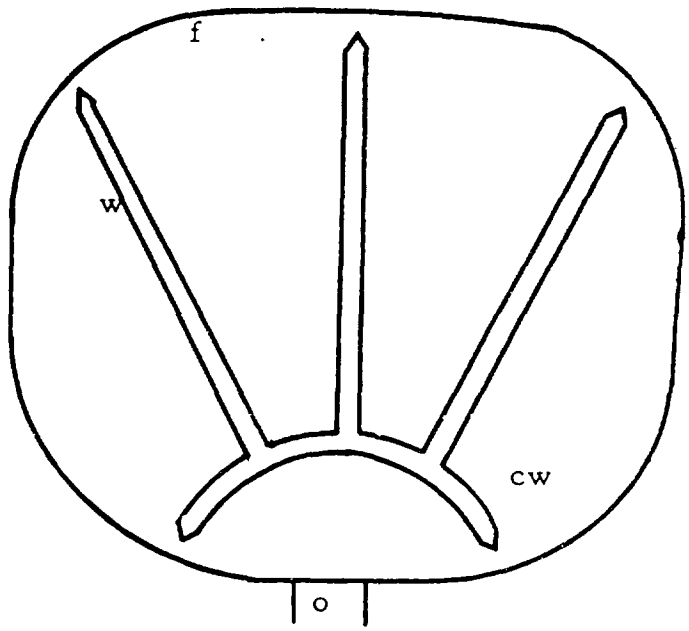

Figure 1. Schematic Drawing of an Outer Enclosure, Top View (w = earthen walls, cw = circular wall, f = fence, o = observation point on building)

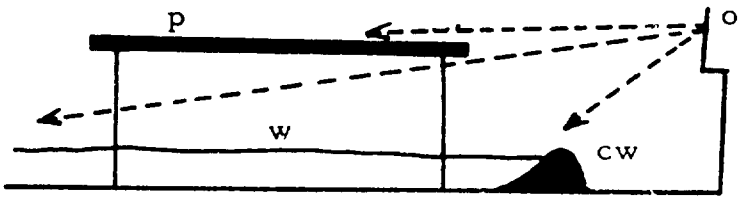

Figure 2. Schematic Drawing of an Outer Enclosure, Side View (w = earthen wall, cw = circular wall, o = observation point, p = platform)

E. Extra Escape Routes

The presence of climbing structures, for example a platform which serves as a sun shelter at the same time, provides a third dimension and gives extra diversification. If it is accessible from several sides it is also a most welcome escape route, particularly since an animal on top can see the pursuing animal below, but not the other way around.

The presence of different escape routes is also very desirable in the dormitory. A pursued animal is much more likely to be caught here, because of the presence of dead corners. If there is only one exit from the hall, it can easily be blocked, especially, if more than one animal is pursuing. The creation of an escape route in the third dimension is even more urgent here than outside. In the usual small inner cages a roof constructed of wire mesh or bars would serve the same purpose.

F. Special Equipment Suited to Discharge Agonistic Tensions

A particular way to decrease the effects of agonistic tensions has been suggested by Kortlandt (1). From all cited field studies it appears that chimpanzees in excitement incorporate in their intimidation displays such activities as drumming on tree butresses, dragging trees to the ground, swinging around branches and throwing objects. These behavior patterns resemble the "redirection" and "displacement" activities, known from many ethological studies of other species to both serve as an effective warning and as a means of discharging built-up tensions. Kortlandt therefore, advises that the enclosures be equipped with materials adequate for this purpose. From my own experience I can recommend resounding objects like metal sheets firmly fixed in a strong frame or rotating drums filled with stones.

G. Moat, Wall or Fence

Kortlandt (2) has already considered the type of separation with which the outer enclosure can be surrounded and has discussed the advantages of moat or wall in connection with the soil structure at the site . Also, see Mottershead (18). Some of the laboratories that have built or are building a compound preferred a fence construction (see Section II.B.2.).

The Consortium at the Holloman Air Force Base is surrounded by a moat with walls sloping down to the deepest point in the middle. The walls are completely smooth and, especially, when grown with algae they become very slippery. It occasionally happened that when an animal fell in, it did not succeed in climbing back and had to be rescued. At the moment the inner slope near the place where the animals are most often has been covered with wire fence and the remaining portion may be covered as well. At the Arnhem Zoo in the Netherlands a similar type of moat is used. Here, two simple vertical stone walls about a foot high have been built on the inner slope at such a distance off the shore that they are completely covered by the water (Fig. 3a). A disadvantage of the vertical walls is that once the animal has grasped the wall and is standing on top, it can attempt to escape in either direction. If the walls have a slanting position (Fig. 3b) or if slanting steps are used (Fig. 3c), the animal can only push itself off in one direction, in this case, back to the enclosure. These are even simpler to build.

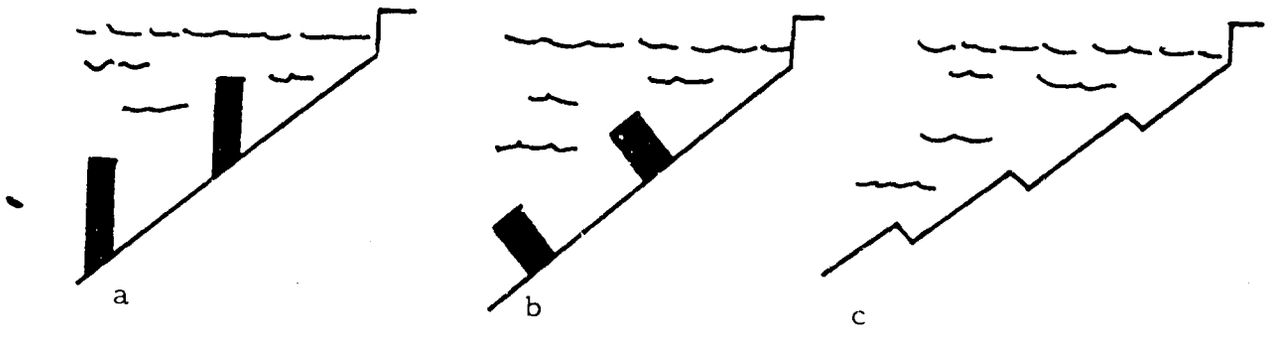

Figure 3. Various Types of Moat Walls (for explanation see text)

The events at the Holloman Air Force Base suggest and my own experience at the Arnhem Zoo indicates, that unexperienced apes show no reluctance to jump into the water. Probably this is especially so when the water is clear and the bottom is visible. After their introduction into the new enclosures all three chimpanzees and both gorillas at the Arnhem Zoo got into it the first days. Only the orangutans never did. After their first experience they seemed to be cured forever. Since we had anticipated this an attendant with a long broom was always present to assist them in their attempts to get back. In several cases where this was not so, chimpanzees were drowned.

The experience with electric shock wires has been very disappointing so far. Both at Holloman and at the Chester Zoo animals have passed such wires. They can do so either by climbing past these very cautiously or by grounding them.

VII

EMPLOYMENT

Both from the wild and from captivity we know that chimpanzees are alert, intelligent and inquisitive animals. These qualities, which more than any others are illustrative of their affinity to us, help them to adapt themselves to a variety of habitats and circumstances. The use and even the making of tools to assist in acquiring certain food items, as described by Merfield (19), Goodall (5, 20), and Izawa and Itani (21) are a beautiful example of this. In the wild they seem to retain these qualities at adult age, much in contrast to what happens in the usual zoo conditions where they get more dull and bored the older they become.

For the sake of the animal's psychological well-being and in order to have animals in optimal conditions for psychological experiments, Kortlandt (1, 2) and Morris (7) recommended that a means be found to give the animals employment. From my own experience I know that this is not so easy. In zoos, employment is usually offered during the daily shows and tea parties. However, only the younger animals participate in these. For the adult animals the problem is greater. Simple "artificial" playing devices, like a ball or a car tire, may capture the animal's attention for some time, but they tend to become bored with these sooner or later.

Only those devices seem to occupy them most fully that (1) have an inherent amount of complexity or variability, (2) permit them to perform some natural activity (e.g. nesting) or (3) , which render a non-devaluating reward:

(1) An example of an object meeting the first condition is a simple gunny sack or a nylon stocking. It can be swung, dragged, thrown, twisted, torn, chewed and used in many different ways to dress up. I would therefore suggest, that old and useless materials and objects which cannot become dangerous when being manipulated by the chimpanzees should end their careers in the chimpanzee cages. It may be well worth some extra mess at times.

(2) An activity that occupies them a great deal in the wild is nest making. I know of two zoos where the animals are given straw or wood wool. In one of these, the London Zoo, one large cage, which

always at least one animal being very much occupied with constructing a nest. This can keep them busy for a long time, especially because, who takes the material to get its turn. In the Consortium at the Holloman Air Force Base, chimpanzees could frequently be seen collecting twigs and other materials to build a nest. It appears to be an unexhaustibly rewarding activity.

The objections raised against the idea of providing nest material were almost always concerned with the extra amount of labor required for providing the material and, even more so, in cleaning it away. Furthermore, it is feared that it may choke up the drains. Objections in connection with the hygiene in the cases rank next. One zoo formerly provided nesting material, but stopped doing so after a female had got a nasty infection by masturbating with pieces of straw. This, however, would seem to be an incidental case. Concluding, I would say that it is well worth reconsidering to what extent the disadvantages are offset by the beneficial influences on the animal's psychological well-being. The disadvantage in connection with the draining system should not seem to be too difficult to minimize.

(3) While discussing the chimpanzee diet it is suggested that the cages be equipped with devices that allow the animals to work for their food. Several types of mechanisms could be devised which serve this purpose and which perhaps, at the same time, by the incorporation of properties found in the common equipment used for psychological experiments, can raise the animal's problem solving capacities. Interesting examples are the coin-operated slot-machines for chimpanzees developed at the Yerkes laboratories which were installed in a cage in the London Zoo (22).

There are mechanically simpler and less costly means as well. One could design a "pseudo termite hill" containing a pill reservoir feeding a vertical tube. Through horizontal tubes which connect with the vertical tube the pills could be collected by means of twigs and other tools. Several variations are conceivable on this theme, i.e. the procurement of food items with the help of implements. If a number of such structures, each involving a different principle were made in such a manner that they could be temporarily fixed in the cages, the inhabitants could have a new problem every so often by exchanging the instruments.

VIII

DIET

A. Food Selection in the Wild

All field studies (4, 5, 6, 20, 21) indicate that the chimpanzee is a very euryphagous animal. The bulk of its diet consists of fruits, leaves, bark and pith. Merfield (19), Goodall (5, 20) and Reynolds and Reynolds (6) mention that they have seen the animals eating insects, and Goodall reports, moreover, to have seen them eating meat on nine occasions. The latter has not been reported by the other investigators. Thus it seems that, although their range of food items is potentially very extensive, certain populations have a more or less restricted range of items. Kortlandt (16) has given evidence that the choice of food items is largely determined by tradition, which in itself is shaped by the conditions at the living site. The animals appear to be very conservative with regard to this tradition. When animals arrive at a food source hungrily they start picking unselectively; the selectivety increases strongly, however, immediately afterwards. Chimpanzees spend much of their time feeding and a substantial part of the remaining time traveling from one food source to the next. Coprophagy, a habit commonly occurring in captivity, was not observed in the wild.

From the wide variation of food consumed by chimpanzees in the wild and their habit of choosing another kind of food almost every moment, Kortlandt concludes . . . "That they have a greater need for diversity of food than any other primate" and that . . . "perhaps one of the main causes of bad conditions in captivity is the monotony of the food usually given." He suggests, therefore, that attempts be made to provide more variation in the diet.

Although extensive lists of food items taken by chimpanzees in the wild have become available through the above mentioned studies, no analysis of the most important items for their contents of carbohydrates, proteins, fats, fiber matter, minerals and vitamines has been undertaken. Nissen, who in 1930 collected some 34 species of plants belonging to the diet of chimpanzees in Guinea, unfortunately saw all of his material destroyed by rats before the contents had been determined.

B. Experimental Studies Concerning the Chimpanzee Diet

Chimpanzee feeding methods and diets in captivity have recently been the subject of extensive research. In zoos these vary widely. Most usual are cereal or eggnog type of broths combined with fresh fruits and vegetables. Commercial pellets were considered adequate nutritionally but not palatable enough as a single item diet. In the majority of primate laboratories commercial pellets were the staple food, supplemented by small quantities of fresh fruits and vegetables (23).

A number of current diets were analysed by Nees, Derse and Robaidek (24) with respect to the levels of vitamines, amino-acids, minerals, fiber, moisture and fat. These appeared to be quite adequate both qualitatively and quantitatively. A biological evaluation of these diets by means of the rat growth assay by Robaidek, Derse and Nees (25) showed that these were quite satisfactory, sometimes even excellent.

The same diets were also evaluated for adequacy during feeding experiments with chimpanzees (26). The intake of nutritients, blood-clinical and biological measurements, nitrogen and calorie balance were compared as well as variations in appetite, playfulness, activity and manageability, and the effect on the habit of coprophagy.

Although the diets provided sufficiently for the basic nutritional needs of the chimpanzee, some interesting differences were found.

1. Variation in the Diet

Thus, one of the pellets that was somewhat sweet and flavored was taken in great quantities initially (except for one chimpanzee that never did eat them); later on, however, the consumption dropped to such an extent that decreased rate of weight gain or even an actual loss was recorded. Thus the animals apparently got tired of it. This did not occur with the unflavored pellets.

This would suggest that variety in the diet is important when food is offered of a prominent taste or smell, but that it is less necessary the more neutral the taste and smell.

2. The Protein Content

The protein contents of the different diets measured as a percentage of the dry weight were 17.4, 17.5, 20.1, 22.0, and 28.0. The

protein contents appeared to be more than sufficient in the first four diets and too high in the last one. When the animals were fed this diet they invariably got diarrhea, which in some cases lasted throughout that trial period. The low protein diets gave good stools. Unpublished work by Hodson (personal communication) shows that a protein content not higher than 16 percent is ideal. However, all commercial products were over this level and his opinion was that also in most zoos the diets were too rich in proteins.

The stools from the other diets were satisfactory. One contained a certain amount of fresh fruits. The feces tended to become a bit loose on this diet. Especially citrus fruits appeared to be laxative. Both factors may be responsible for the frequent complaints about diarrhea in zoos. In one of the diets a certain amount of fiber mass was included. This diet returned firm stools.

3. Coprophagy

The presence of fibrous material was interesting in another respect as well, since it inhibited coprophagy. The reasons for this behavior generally given are boredom, the natural habit, the presence of an attractive element in the feces under certain conditions and the desire of the animal to hold a mass of roughage in its mouth to chew on. Boredom can be excluded in this experiment, because the animals were isolated for almost the whole day during all of the experimental period. Yet the behavior was completely absent during certain diet trial periods and prominent during others.

It is known from the wild (12, 20, 21) that chimpanzees devour much roughage. When eating fruits or eggs they will regularly pick leaves and chew these with the other food stuff. They may keep this wadge of chewed leaves in their mouth for long periods, regularly chewing and inspecting it. Goodall (20) noted that the animals would steal pieces of cloth to use as a wadge. Izawa and Itani (21) saw them use strips of bark as "chewing gum." Since the diet with high fiber content was of the right nature to form a wadge and inhibited coprophagy, the reason for this habit may well have been hit upon.

Nees, Derse, Robaidek and Regel (26) mention one other cause as well. Of the other "non-fibrous" diets those feces were handled and eaten most frequently that were more odoriferous. One may conclude from this that it should not be too difficult to overcome this habit, a matter of concern to every zoo director.

4. Psychological Condition

It is also of interest to note that the animals were least manageable and playful and sometimes most irritable during the trials with diets that were least satisfactory in other respects. The flavorless diets giving firm stools produced satisfied, playful and cooperative animals.

The results of these studies indicate that variation as such is not necessary, provided that the food meets the above mentioned requirements. This is not to say, however, that in conditions where the animal has to be isolated the feeding routine could not be made more of an event by variation or by installing machines that require the animal to work for its food. In a poor environment this could well mean the difference between a bored and an alert animal.

IX

CLIMATOLOGICAL CONDITIONS

Chimpanzees live in an extensive area which stretches from the south of Senegal all along the Gulf of Guinea to Congo Brazzaville. It stretches further eastward through the north of Congo Leopoldville, the south of the Central African Republic and the southwest of the Sudan to Uganda and from there extends southward to Lake Tanganyika (12) Only 55 percent of the original geographical range consists of the tropical rain forest; the remainder varies from montane vegetation types via forest-savanna mosaics to relatively dry types of woodlands and savannas (27, 12). In the latter types of habitats where they are most easily hunted they have become very rare or virtually exterminated almost everywhere, except in some areas in Guinea. Both as far as vegetation type as well as humidity is concerned they appear to tolerate a very broad range of environmental conditions. At least in Guinea the relative density of the chimpanzees is influenced mainly by vegetational aspects and human influences. The climatological factor only seems to be of influence where it limits the western range by a total lack of water during a great part of the year (27).

In Table VII I have collected a few characteristic climatological figures for a number of meteorological stations at various points within (or perhaps quite near) the chimpanzee range. It appears that the monthly averages of the daily measurements (around noon) of the relative humidity can vary greatly.

A. Sensitiveness to High Temperatures

Chimpanzees are found in areas where maximum temperature of more than 40° C and maximum monthly averages of the measurements of the daily maxima of 37 and higher have been recorded (Table VII). High temperatures occur mainly on the northern edge of the range, namely in dry inland areas of savanna type of low to moderate elevations, whereas in tropical rain forests in coastal regions, around the Congo Basin and, particularly, in regions of high elevation, temperatures are only moderately high.

Both Nissen (3) and Kortlandt (12) mention, nevertheless, that chimpanzees seem to be very sensitive to high temperatures. They found that chimpanzees are not active during the hot hours of the day. In Guinea and

Sierra Leone they avoid open spaces and withdraw in ravines and gallery forests between 10 a.m. and 4 to 5 p.m., i.e. when temperatures are above 26 to 28°C. It was Kortlandt's impression that they do not feel comfortable when the temperature is above 23°C; They then often walk with a wide-open mouth, in much the same way as dogs do in hot weather, except that chimpanzees do not pant visibly. It is not clear whether the apes are sensitive to air temperatures above the mentioned level as such, or specifically to the radiant heat of the sun which is maximum at the same time. The latter is more likely since with their black skins and coats they strongly absorb radiation. In this case they might be able to stand comparatively higher temperatures in the shade.

With respect to the heat sensitiveness there seems to be a contradiction between the meteorological and the behavioral data. One should note, however, that the meteorological figures represent "anthropomorphic" temperatures taken in towns and on airfields. The "chimpomorphic" temperatures, i.e. taken at the places the apes spend the hot hours (cool ravines or gallery forests) can be very different. A number of pairs of measurements taken in the open field and in the forest respectively at about the same time at night or during the day have been plotted in Figure 4. These show that the differences between the members of the pairs of day measurements increase progressively the higher their average temperature, and that the temperature gets lower the deeper one penetrates in the forest. At night, on the other hand, the temperatures in the forest are not as low as in the savanna. Thus it is likely, that even in areas that are hot by meteorological standards, the temperature rises rarely over 27°C in the places where the apes spend the hot hours.

B. Sensitiveness to Cold

The average minimum temperatures are usually higher than 15°C, except for areas of high elevation. The lowest absolute minimum temperature recorded officially is 3.9°C. Kortlandt has noted that chimpanzees at Beni slept without cover, many in treetops, during strong winds and rains while the temperatures were as low as 15°C. The apes do occur on the slopes of Mount Cameroun, and the Ruwenzori at heights at 6400 and 9000 feet respectively, where they must be regularly exposed to minimum temperatures of 4 to 7°C. On the latter mountain they may experience occasional night frosts.

TABLE VII. Temperature at Various Meteorological Stations Within the Original Geographical Range* **

Column a: The average of the yearly maximum temperatures.
Column b: The highest value of the monthly averages of the daily maxima.
Column c: The lowest value of the monthly averages of the daily minima.
Column d: The average of the yearly minimum temperatures.
Column e: The highest value of the monthly averages of the daily relative humidity figures measured around noon or early in the afternoon.
Column f: The lowest value of the monthly averages of the daily relative humidity figures measured around noon or early in the afternoon.

	a	b	c	d	e	f
MALI, Guinea 12°N-12°W; Elevation 187 ft	39	28	15	7	95	43
KOUROUSSA, Guinea 11°N-10°W, 1217 ft	43	38	16	4	73	19
CONAKRY, Guinea (coast) 10°N-14°W; 23 ft	36	32	22	17	87	63
FERKESSÉDOUGOU, Ivory Coast (N) 9°N-5°W; 1102 ft	41	34	16	10	80	28
BOUAKÉ, Ivory Coast (center) 8°N-5°W; 1194 ft	40	34	20	14	79	55
ABIDJAN, Ivory Coast (coast) 5°N-4°W; 65 ft	36	32	22	15	82	71
TAMALE, Ghana (N) 9°N-1°W; 635 ft	41	37	20	15	74	20
KUMASI, Ghana (center) 7°N-2°W; 942 ft	38	33	20	11	79	56
YOLA, Nigeria (N-E) 9°N-12°E; 707 ft	43	39	17	11	69	15
KOUNDJA, Cameroons (mountains) 6°N-11°E; 4000 ft	33	29	15	12	73	29
KRIBI, Cameroons (coast) 3°N-10°E; 43 ft	33	31	21	19	86	77

(Table VII Cont'd)

	a	b	c	d	e	f
LOANGO, Congo Brazzaville (coast) 5°S-12°E; 164 ft	34	31	19	15	79	73
FRANCEVILLE, Congo Br. (S) 2°S-14°E; 1398 ft	34	31	18	13	73	64
OUESSO, Congo Br. (N) 2°N-16°E; 1132 ft	41	33	21	16	73	68
BOUCA, Central African Republic 6°N-18°E; 1503 ft	42	37	13	9	71	26
BRIA, Central African Republic 6°N-22°E; 1916 ft	41	36	18	8	72	33
BARUMBU, Congo Léopoldville 1°N-23°E; 1378 ft	37	32	19	15	90	82
BAMBESA, Congo L. 3°N-26°E; 1969 ft	39	32	17	10	70	51
FORT PORTAL, Uganda 1°N-30°E; 5049 ft	31	27	12	7	70	55
TSHIBINDA, Congo L. 2°S-28°E; 6939 ft	27	22	9	5	69	51
ALBERTVILLE, Congo L. 6°S-29°E; 2493 ft	33	31	14	10	75	59

* Temperature in degrees centigrade.

** Data taken from "Tables of temperature, relative humidity and precipitation for the world." Meteorological Office, Air Ministry M.O. 617d, London 1958.

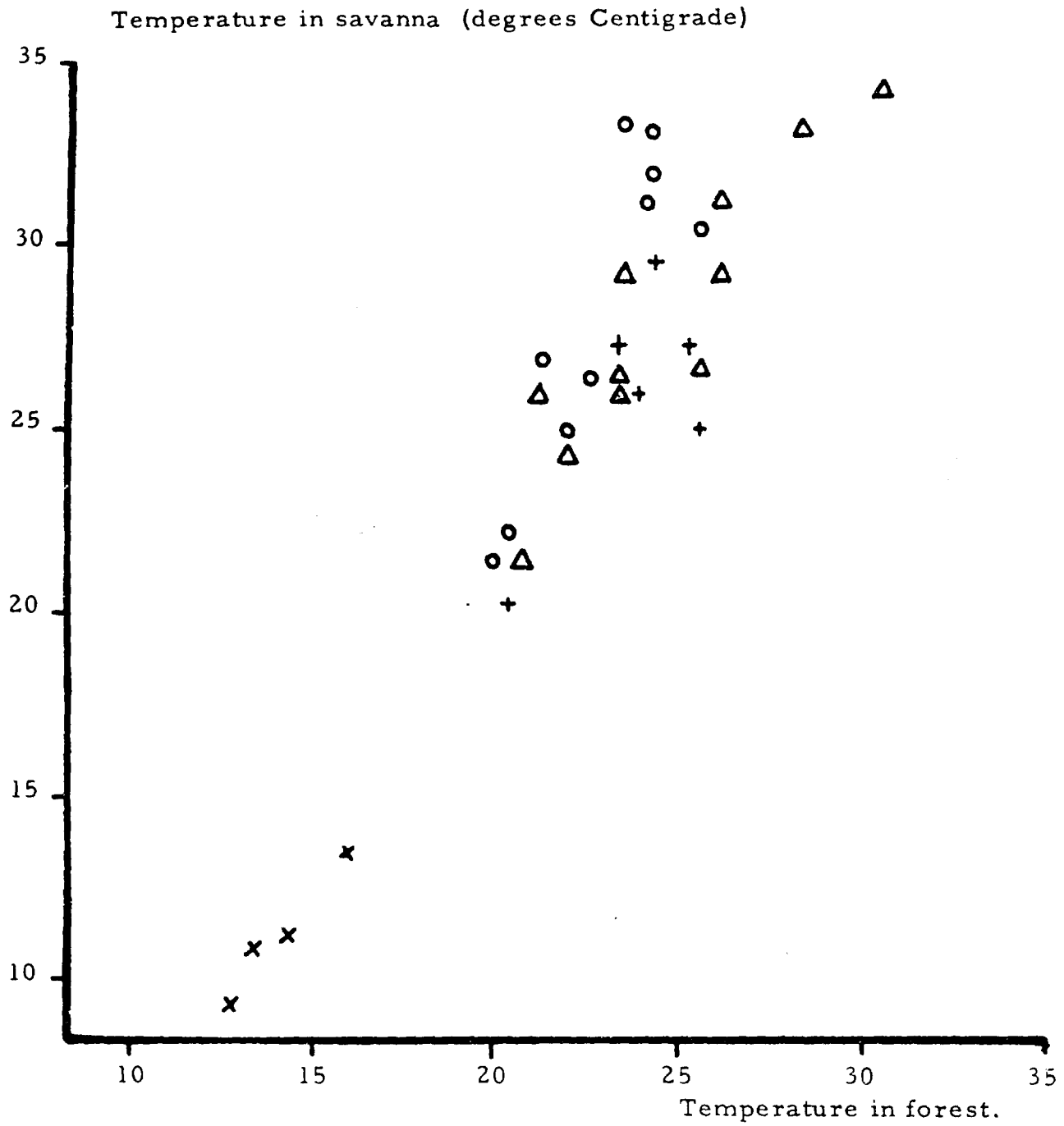

Figure 4. Temperature Chart

Each point represents a pair of more or less simultaneous temperature measurements in the savanna and in a near forest.

o = "open savanna" versus "deep inside forest"
Δ = "open savanna" versus "just inside forest" or "edge of savanna" versus "deep inside forest"
\+ = "edge of savanna" versus "just inside forest"
x = "minimum temperatures during the night" (from Kortlandt, unpublished field notes)

C. Temperature Conditions in Captivity

Many zoos keep the inner quarters of the apes at about 20 to 25°C. The animals are permitted to go outside for long periods only on relatively warm, dry days. Thus they are treated carefully with respect to cold weather. On the other hand, it is still possible to encounter zoos where the chimpanzees on hot summer days are shut outside in cages which offer only limited shade.

Kortlandt (2) suggested that in the selection of sites and the designing of cages for primate centers the heat sensitivity has not been considered sufficiently.

Table VIII presents the temperature data for the area of four primate laboratories where summer temperatures are high. Comparison of the figures shows that the maximum temperatures and the maximum monthly averages of the daily maxima of the Holloman Air Force Base and the San Antonio Primate Laboratory, Austin, Texas, are comparable with those of the savanna meteorological stations, with medium high maxima, whereas Yerkes Regional Primate Research Center, Atlanta, Georgia and the Delta Regional Primate Center, Covington, Louisiana, have comparatively moderate average maximum temperatures. These are still high if we take into account that chimpomorphic maxima in the wild are considerably lower than the measured maxima. A comparable situation would exist when the animals, the great majority of which have their outer cages fully exposed to the sun (see Section II) can withdraw in shady places which are about 5°C cooler. In two of the laboratories this can easily be achieved because the halls containing the inner cages are air-conditioned. In the other one, the hall containing the inner cages is not air-conditioned but is nevertheless cooler than outside. During an afternoon visit I measured outside 28°C and inside 24°C. So the animals should be enabled to withdraw in the inner cages during the hot hours. This was possible, except in one case because exactly during that period the inner cages were being cleaned.

D. Compounds Shaded by Trees or Artificial Shelter

One compound, intended for small chimpanzees, was shaded by many trees. Another was grown over with trees originally but these had all died owing to the activities of the inhabitants. A small one-story building annex to this compound was the only sunshelter left, but it was not very cool. The third and largest compound had been planted with trees but none had survived the activities of the chimpanzees.

These experiences and those of a few zoos indicate that there is little hope that trees can provide a large shadowy area for an appreciable length of time, unless the animals can be shifted to a new area from time to time in order to permit the trees of the formerly occupied areas to regenerate. This would imply, however, that a large terrain is available. A solution might be to erect a sunshelter in the form of a large platform on columns. It should be high enough so that it does not get too hot underneath. If it were constructed in such a manner that the animals could sit on top of it, it could at the same time serve as an extra escape route and an extension of the living space (see Section VI. D. and VI. E.).

TABLE VIII. Characteristic Climatological Figures for Areas in Southern United States where a Laboratory is Keeping Chimpanzees* **

	a	b	c	d	e	f
NEW ORLEANS, La. 30°N-90°W; 8 ft	36	32	8	3	69	61
ATLANTA, Ga. 34°N-84°W; 1054 ft	39	31	2	-22	66	54
AUSTIN, Texas 30°N-98°W; 615 ft	43	35	4	-18	62	42
HOLLOMAN A.F.B., N.Mex. 33°N-106°W; c. 4000 ft	c. 42	34	-2	c. -20	g 41	h 22

(g = highest monthly mean relative humidity; h = lowest monthly mean relative humidity).

* Legend same as Table VII, page 43.

** Data of Holloman AFB from local meteorological office. Other data from same source as Table VII.

X

THE STANDARD OF CHIMPANZEE CARE

The condition of captive chimpanzees depends, not only on the aspects mentioned above, but also to a large extent on the standard of care. It is difficult to judge objectively and would certainly justify a separate study. Although it is beyond the scope of this report, I may, nevertheless give my opinion.

According to my experience with zoological gardens the hygienic conditions and the amount of effective veterinary control still vary greatly in European zoos. It is likely that a similar situation exists in the rest of the world. My experience with American zoos is restricted to a superficial impression of three of high standard. The hygienic conditions in primate centers seem to equal or exceed those found in zoos, perhaps partly because their more uniform character favors a more systematic approach and also because a more or less extensive scientific staff is in close touch with the animals.

In zoos, more than in laboratories, the immediate responsibility for the daily care rests with the animal keepers. The effectiveness of various measures, for instance hygienic ones, depends on the way they carry these out. By their close and continuous contact with their animals they are moreover in an excellent position to observe any developments. Therefore, both training and experience is important. A standard training, including basic theoretical education, for the animal keeping profession is easiest realized in connection with laboratory animal keeping. This has been done in several countries already. As far as I know, however, there are no general standardized courses for zoo keepers. As each keeping job in a zoo has its own routines and problems, the experience is often passed directly from one keeper generation to the next (i.e. from father to son). Intuition is still an important factor in the profession and an experienced keeper may carry great authority, and rightly so. Yet the lack of a very elementary scientific training may hamper the effective introduction of scientifically inspired changes in methods. A basic scientific training would certainly be no luxury. It would naturally have consequences both for the status of the job and financial aspects.

According to Kortlandt (2) the present American animal keeper compares unfavorably with his non-Latin European colleague both in his educational level and his salary. From data supplied to me no difference appeared, however. Both in Europe (Germany and the Netherlands) and the United States salaries appeared to vary according to age, experience, responsibility etc., between institutes and also within institutes. It is difficult to get a good impression, therefore.

XI

CONCLUSIONS

In Section I, Introduction, a number of points were discussed that were regarded as indications that the present methods of keeping chimpanzees are not fully adequate, particularly from an ecological point of view, resulting in a physiological and especially psychological condition of the animals which is below optimal. In contrast to what is reported from the wild, many captive animals become apathic and dull, indulge in stereotypic behavior patterns and become very aggressive and impredictable the older they get. The fact that the present reproduction rate in captivity appears much too low to make a continuous importation from the wild superfluous was also regarded as significant in connection with the conditions of captive chimpanzees; whether this is justified remains questionable, as we shall see. Both these points and their causes as well as possibilities for improvement have been considered in this report.

A. Existing Housing

The existing housing conditions are to a large extent comparable in zoos and laboratories. The great majority of animals are housed in relatively small cages which on the average can contain two to three adults at the most. A minority are housed in large compounds, four of which have been described here (one is still under construction). In only two of these is the housing of a group of more than about ten adult apes possible.

B. Lack of Social Stimulation

If highly social animals with variable and boisterous interactions like chimpanzees are kept solitary or in pairs, the resulting lack of social stimulation could lead to dullness, apathy and neurotic behavior, the more so since diverting and alerting incentives offered by possibilities for manipulation and investigation are lacking as well. Undoubtedly their psychological condition could be much improved by keeping them in larger groups.

C. The Level of Aggressiveness

The fear that keeping chimpanzees in social groups in captivity is impossible or dangerous owing to aggression, appears to be largely unjustified. Although the level of aggressiveness in the one captive group

studied was certainly higher than in the wild groups studied it was not so serious as to form an impediment. The difference could be explained as a result of the following factors:

(1) Food Competition. This is practically absent in the wild. In captivity it could be minimized by distributing the food over a large area and/or by isolating the animals at feeding time.

(2) Specific Antipathies. In the wild these would not find expression because the animals can avoid one another easily enough. In captivity a group should therefore be composed carefully to avoid joining of animals with strong mutual antipathetic tendencies. Recombination of groups of animals may be easier in a laboratory where there are usually many more animals available than in a zoo which can have only a limited stock as a rule. In addition, visual barriers could be provided to establish some privacy in the cage.

(3) Disturbances in Social Adjustment. These could result from traumatic experiences while growing up in captivity and from the lack of necessary social experiences normal for chimpanzees growing up in the wild. Capturing groups with a common social tradition instead of isolated babies may be an improvement. Animals born in captivity should have ample opportunity to gain social experiences and to get in touch with the social tradition. Most ideal would be to let them grow up with the mother in the group. However, if one wants to get a maximum natality, this is less advantageous than a separation of mother and young at an early stage (see below). How this dilemma should be solved, depends largely on the purpose for which the animals are being kept.

D. Reproduction in the Wild and in Captivity

In the wild there is, as a rule, a balance between natality and mortality. A considerable proportion of the accrescence of the captive population, however, appears to consist of imported young animals. This could indicate that in captivity the balance between natality and mortality is greatly disturbed owing to the bad psychological and physiological conditions of captive chimpanzees. An alternative explanation is possible, however.

The natality in captivity appears to be, on the whole, somewhat lower than in the wild, though not dramatically so. The difference could have the following causes:

(1) Increase in Zoos and Research Centers. The increase in the number of zoos and research centers is almost certainly correlated with an increase in the chimpanzee population in captivity. It will therefore be comparatively young and contain fewer reproductive animals. This is certainly an important factor for explaining the comparatively lower natality rate. The zoo population is very much split up, moreover, so that a number of animals may be withdrawn from the reproduction process by lack of a suitable sex partner.

(2) Social Maladjustment. This may express itself in unsuitability for the reproduction process. The aggravation of its effect by the division of the zoo population has been discussed above.

(3) The Social Stimulation of Sexual Behavior. Certain stimulating factors characteristic for large bi-sexual aggregations that are important normally for the elicitation of the riot-like sexual interactions in the wild, may be absent when only two or three animals, completely accustomed to one another, are constantly together. The fact that there is nevertheless considerable breeding in captivity shows that these factors are not or not always indispensable.

It appears questionable whether the influence of the psychological factors will appear to be very considerable after the influence of the peculiar characteristics of the zoo population (age composition, growth, division) has been accounted for.

Improvements in connection with the factors mentioned, apart from the, in this respect, irrelevant influence of the population growth, can be achieved by keeping the chimpanzees in large social groups, especially if the groups are captured as such in the wild. Natality could also be stimulated by removing the baby from the mother immediately after birth, so that the mother can have another baby the following year. Besides, in the Yerkes Laboratories the mortality amongst youngsters reared artificially was lower than amongst those growing up with the mother (Bourne, personal communication). Here again, however, the problem of social development arises.

The total reproduction is also a function of the mortality. Very little is known about it, but there are data suggesting that it is still considerable, also in the younger age classes. A serious consideration of this problem could be very rewarding.

E. Social Groups

Large social groups could best be housed in a setup consisting of units which apart from a large open enclosure and one or more dormitories for normal use, contain a number of small conventional cages permitting isolation of the animals. Such a setup would minimize the objections to keeping large social groups, especially in connection with the requirements for experimental work in laboratories.

F. Intellectual Employment

Boredom may be a threat especially for captive animals kept solitary or in small groups, living in small and "clean" cages. Different types of employment which could be provided have been considered.

G. Diet

Experiments have been discussed which show that variation of diet is not necessary as long as it has a neutral taste or smell (provided, of course, that it meets the nutritional requirements). Animals getting a qualitative better diet returning firm normal stools appeared to be in a better psychological condition as well. Coprophagy appeared not to be a matter of boredom; in isolated animals it could be prevented by giving a diet containing a certain amount of fibrous material and/or rendering a not too odoriferous feces.

H. Sensitiveness to High Temperatures and Strong Sun Radiation

Chimpanzees seem not to like excessive heat and void exposition to strong sun radiation. They should be able to withdraw in a shady and, if possible, cool place during the hot hours of the day. The construction of large platforms in bigger enclosures serving as sun shelters is advised instead of planting trees.

I. The Standard of Chimpanzee Care

Hygienic conditions as well as the amount of veterinary control vary greatly in various European zoos. A similar situation may exist elsewhere. In both respects the primate centers would appear to excel. A difference in training between American and European animal keepers has not been found.

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13. ABSTRACT

There are indications that present methods for the care and management of captive chimpanzees are not fully adequate, particularly from an ecological point of view, resulting in a physiological and especially psychological condition of the animals which is below optimal. In contrast to what is reported from the wild, many captive animals become apathic and dull, indulge in stereotypic behavior patterns and become very aggressive and impredictable as they get older. The fact that the present reproduction rate in captivity appears much too low to make a continuous importation from the wild unnecessary was also regarded as significant in connection with the conditions of captive chimpanzees. These points and their causes as well as possibilities for improvement are discussed in this report.

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